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# An Analysis of Some Meristic Characters of the Staghorn Sculpin *Leptocottus armatus* Girard[1]

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ABSTRACT: Over a 4-year period, juvenile specimens of *Leptocottus armatus* were collected annually at nine stations along the Pacific coast from approximately 37 to 47° N latitude. Collecting was repeated at intervals at two stations (43°24′ N and 44°36′ N) during the seasons in which young fish were arriving from the plankton. Meristic character counts are similar over the northern part of the range studied, but there is a well-defined cline in conditions south of 43° N. The number of spines on the dorsal fin appears to be influenced very little by natural developmental conditions, if at all. At the two stations sampled at approximately monthly intervals, well-defined seasonal trends in meristic character counts appear to be related to thermal history. Freedom of independent expression of meristic characters in response to the natural developmental environment is restricted by timing of phenocritical periods and a factor of a more fundamental nature, presumably genetic.

MERISTIC CHARACTERS of fishes are those having serially repeated elements, such as fins with rays and spines, or the spinal column of vertebrae. Such a character can be described by signifying the number of its elements.

During the second half of the nineteenth century evidence accumulated that indicated an inverse relationship between habitat temperature and vertebral number in fishes. So consistently did this relationship appear that Jordan (1891) offered the suggestion that it be termed a natural "law"; the phenomenon is sometimes referred to as "Jordan's rule." Jordan credited Albert Günther with the first of such observations among members of the family Labridae, equatorial species having 24 vertebrae and temperate latitude species of both hemispheres having vertebral counts greater than 24.

Since interspecific variation through a geographical temperature gradient was consistent with Jordan's rule, it was generally assumed that intraspecific vertebral variation could similarly be taken to represent racial differences in populations as, for example, those of the European herring (Heincke 1898). However, the experimental studies of Schmidt (1917, 1919, 1920, 1921) demonstrated a degree of ecophenotypic plasticity that had not been suspected previously. The number of elements in a given meristic character is to a considerable degree susceptible to the effects of developmental environment, particularly temperature.

Tåning (1952) reviewed the experimental work on salmonids that demonstrated well-defined phenocritical periods in the course of development during which numbers of elements in meristic characters are influenced by temperature. His work showed that each of the characters has its own phenocritical period(s). Tåning summarized his work and others' which showed that the phenocritical period of vertebral number occurs at gastrulation, with a later period shortly before the eyed stage, and that the phenocritical periods of the dorsal and anal fins occur later. Experiments on the development of salmonids were extended and refined by Orska (1962), who found that the number of somites is influenced by developmental temperature throughout gastrulation. The work of Lindsey (1954) showed that vertebral number

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may continue to be susceptible to environmental effects beyond gastrulation.

Heuts (1949), working with sticklebacks, found that in comparing groups of experimentally reared fish, the variance of the mean number of fin rays could be taken as an indicator of whether differences in means resulted from selective mortality or were caused by developmental response to environmental conditions.

Meristic characters of *Istiblennius edentulus* were described by Strassburg (1955), based on a study of specimens collected from the Marianas to the Gambiers Islands. He found that the fin ray counts increased with increase in latitude to each side of the equator. Here, an intraspecific parallel of Günther's original observations is seen.

From studies of darters of the genus, *Etheostoma*, Strawn (1961) found that numbers of scales in the lateral line and of rays in the anal and dorsal fins could be influenced by temperature throughout the free-swimming period of larval development. As had Heuts (1949), Strawn concluded that in laboratory-reared populations, "high variances probably correlate with environmental factors rather than with genetic differences" (1961:156). This seems reasonable since the conclusion was based on the fact that the highest variance in meristic character counts was found in experimental lots that had suffered the greatest mortality.

After an extensive study of *Sprattus*, Lindquist (1968) concluded that in natural populations the degree of environmentally induced variation in number of vertebrae is so great that this character is not likely to be useful in distinguishing races or populations.

The species investigated in the present work was studied by Hubbs (1921), who described a cline in numbers of soft rays in the vertical fins. Hubbs considered specimens collected from Port Mulgrave, Alaska, to San Diego, California. A well-defined break in the cline occurred at about Santa Cruz, California, and Hubbs concluded that the populations south of that locality constituted a distinct subspecies. He designated the two subspecies as *Leptocottus armatus armatus* and *Leptocottus armatus australis*.

Jones (1962) presented a life history study of *L. armatus armatus* based on findings in the region of San Francisco Bay. He found that this species has a long spawning season, beginning as early as October and with a peak in January or February. Work preliminary to the present study indicated that spawning along the Oregon coast could be expected as early as October, with the season extending at least into January. However, Pearcy and Myers (1974) found planktonic larvae of this species in the lower estuary of Yaquina Bay from August through March. Hence, in some years the spawning season begins much earlier than was believed when the present study was initiated. Jones (1962) took ripe adults from trawls in San Francisco Bay, where I assume spawning takes place, although the natural spawning habitat has not been reported. Eggs of this species are laid in demersal clusters. Unlike planktonic eggs, those of sessile nature may be subjected to some degree of environmental vicissitudes. Upon hatching, the larva of *L. armatus* seeks surface strata where conditions are different from those under which embryonic development occurs.

In September 1949 and October 1951, I found ripe specimens of *L. armatus* in squid catches taken by lampara fishermen a few miles offshore from Monterey, California. On 26 March 1952, I collected *L. armatus* larvae from surface waters of Monterey Bay, California. A number of these larvae were maintained in the laboratory and underwent metamorphosis approximately 4 weeks later. Finding gravid adults and larvae in such an open bight as Monterey Bay suggested that after hatching, the larvae might be transported along the open coast for considerable distances during their planktonic tour.

Studies of eggs and larvae of *L. armatus* indicate that at temperatures of about 9 to 12° C, embryonic development would require approximately 2 to 3 weeks and planktonic larval development about 8 to 10 weeks. Metamorphosis may occur when the animal is about 10 to 20 mm in standard length. Some juveniles having a standard length of more than 30 mm are found to have bright silver ventral surfaces, indicating a planktonic tour of longer duration. It seems probable that metamorphosis is, to a considerable extent, induced by suitable habitat. As has been reported by Jones (1962), with the approach of metamorphosis the young are strongly attracted by freshwater and they strike the bottom on estuarine mud flats in the mouths of small streams.

The present study of *L. armatus* was undertaken to learn the extent of variation in latitudinal cline in meristic character conditions from year to year and among collections of juvenile recruits taken at different times during the seasons in which they were arriving from the plankton. Analyses of the data have also shown some interesting relationships between the meristic characters.

## METHODS AND MATERIALS

Eighty-one collections comprising a total of 10,307 juvenile specimens were studied. They were taken during the period from 9 January 1959 to 16 June 1962. Small seines were used to collect specimens over mud flats under the influence of freshwater. The fish were preserved in 10 percent formalin and remained in that fixative for a few days. They were then cleared and stained according to the directions of Clothier (1950).

The following data were recorded for each specimen: standard length to the nearest 1.0 mm; spines in the dorsal fin; soft rays in the dorsal fin; soft rays in the anal fin; trunk vertebrae; caudal vertebrae; total of the two vertebral counts.

The vertebrae were counted on the basis of the number of neural arches, with the urostyle taken as the terminal vertebra. Caudal vertebrae, to include the urostyle, were taken as those bearing hemal spines. Only the total number of vertebrae is considered here, because there is little variation in the number (11) of trunk vertebrae. Statistical procedures used in treatment of the data are those of Snedecor (1946). Graphic presentations in Figures 1, 2, 4, and 5 approximate the method of Hubbs and Hubbs (1953) to facilitate statistical comparisons. In these graphs, a base line defines the range and a mark on the line indicates the mean. A bracket extends one standard deviation ($s$) in each direction from the mean. The solid area within the bracket extends two standard errors ($2s_{\bar{x}}$) to each side of the mean. In comparing two samples, if the solid areas do not overlap, the value of $P \leqslant 0.01$. This level of $P$ is accepted as statistically significant and throughout the work, in the interest of brevity, discussion is confined to this level of confidence. The fish collections are listed in Table 1.

## OBSERVATIONS

### *Size of Fish*

Sizes of fish studied are listed in Table 1. In the first 2 years of collecting, all the animals taken were considered. In the last 2 years, from collections that contained more than 100 specimens, only the 100 smallest were cleared, stained, and subjected to further study.

Monthly collecting trips to the Yaquina, and Charleston, Oregon, sites were begun in November of each year, but only in the third year were recently arrived juveniles found that early in the season (collection 66, 26 November 1960). The size data indicate that recent arrivals from the plankton are not numerous on the mud flats later than about early June.

The last column of Table 1 gives the zero-order correlation coefficient, $r_{15}$, indicating the degree and nature of the relationship between number of vertebrae and standard length. Reference to the critical values of $r$ listed in Table 3 shows that a significant relationship between vertebral number and length is found only in collections 9, 12, 14, and 40. Note that in all four instances, the coefficients are negative. Three of the four collections showing a significant correlation between vertebral number and length were taken at the three northernmost stations within a few days of each other. Specimens in the 77 collections in which $r_{15}$ is not significant were apparently of such mixed origins and histories that a relationship did not materialize. The practice of retaining only the 100 smallest specimens in any collection

TABLE 1

GENERAL INFORMATION AND DATA CONCERNING SIZES OF FISH IN THE COLLECTIONS STUDIED

| FILE NUMBER | $N$ | NORTH LATITUDE | LOCALITY | DATE | STANDARD LENGTH (mm) Range | Mean | $s$ | $r_{15}$ |
|---|---|---|---|---|---|---|---|---|
| 1 | 100 | 44°36′ | Yaquina, Ore. | I/9/59 | 15–42 | 23.39 | 4.87 | 0.122 |
| 2 | 97 | 43°24′ | Charleston, Ore. | I/10/59 | 18–67 | 32.23 | 11.98 | −0.133 |
| 3 | 64 | 44°36′ | Yaquina, Ore. | II/6/59 | 17–63 | 33.38 | 8.96 | 0.222 |
| 4 | 92 | 43°24′ | Charleston, Ore. | II/7/59 | 15–57 | 29.58 | 7.09 | 0.190 |
| 5 | 209 | 44°36′ | Yaquina, Ore. | III/6/59 | 17–36 | 24.67 | 3.80 | 0.006 |
| 6 | 158 | 43°24′ | Charleston, Ore. | III/7/59 | 11–49 | 23.02 | 9.30 | −0.001 |
| 9 | 621 | 44°36′ | Yaquina, Ore. | IV/3/59 | 9–27 | 18.82 | 4.27 | −0.140 |
| 10 | 493 | 43°24′ | Charleston, Ore. | IV/4/59 | 10–31 | 19.17 | 6.14 | −0.084 |
| 12 | 177 | 46°54′ | Grays Harbor, Wash. | IV/6/59 | 9–42 | 17.94 | 6.87 | −0.203 |
| 14 | 244 | 46° 0′ | Seaside, Ore. | IV/7/59 | 10–39 | 18.43 | 5.81 | −0.294 |
| 15 | 276 | 41°48′ | Crescent City, Ca. | IV/19/59 | 9–42 | 18.18 | 7.35 | −0.108 |
| 16 | 107 | 40°48′ | Eureka, Ca. | IV/21/59 | 8–48 | 33.63 | 8.63 | 0.179 |
| 17 | 85 | 39°30′ | Fort Bragg, Ca. | IV/22/59 | 11–42 | 30.69 | 8.41 | −0.105 |
| 18 | 314 | 38°18′ | Bodega Bay, Ca. | IV/23/59 | 9–40 | 21.11 | 7.11 | 0.006 |
| 19 | 215 | 37° 0′ | Santa Cruz, Ca. | IV/24/59 | 11–38 | 19.45 | 4.08 | −0.080 |
| 20 | 423 | 44°36′ | Yaquina, Ore. | V/1/59 | 9–36 | 21.61 | 4.48 | −0.076 |
| 21 | 311 | 43°24′ | Charleston, Ore. | V/1/59 | 10–39 | 23.28 | 4.23 | −0.024 |
| 22 | 184 | 44°36′ | Yaquina, Ore. | VI/5/59 | 10–43 | 33.77 | 3.77 | −0.053 |
| 23 | 226 | 43°24′ | Charleston, Ore. | VI/6/59 | 21–44 | 32.47 | 5.25 | 0.084 |
| 31 | 104 | 43°24′ | Charleston, Ore. | VII/7/59 | 19–56 | 44.72 | 7.14 | 0.030 |
| 32 | 44 | 44°36′ | Yaquina, Ore. | VII/9/59 | 21–55 | 40.25 | 8.42 | 0.011 |
| 34 | 51 | 44°36′ | Yaquina, Ore. | VIII/11/59 | 44–74 | 57.12 | 7.59 | −0.116 |
| 36 | 114 | 44°36′ | Yaquina, Ore. | XII/4/59 | 13–32 | 21.59 | 4.75 | −0.188 |
| 37 | 120 | 44°36′ | Yaquina, Ore. | I/9/60 | 16–34 | 23.66 | 5.07 | −0.067 |
| 38 | 57 | 43°24′ | Charleston, Ore. | I/23/60 | 11–47 | 27.86 | 7.54 | −0.050 |
| 39 | 97 | 44°36′ | Yaquina, Ore. | II/6/60 | 16–36 | 26.21 | 4.89 | 0.000 |
| 40 | 54 | 43°24′ | Charleston, Ore. | II/7/60 | 12–45 | 24.37 | 10.84 | −0.531 |
| 41 | 212 | 44°36′ | Yaquina, Ore. | III/2/60 | 13–38 | 20.04 | 4.02 | −0.111 |
| 42 | 111 | 43°24′ | Charleston, Ore. | III/5/60 | 17–33 | 23.19 | 3.14 | 0.038 |
| 43 | 110 | 44°36′ | Yaquina, Ore. | IV/2/60 | 15–39 | 26.47 | 6.27 | 0.009 |
| 44 | 114 | 43°24′ | Charleston, Ore. | IV/4/60 | 10–40 | 22.92 | 7.83 | 0.011 |
| 45 | 95 | 44°36′ | Yaquina, Ore. | IV/4/60 | 17–44 | 30.32 | 5.63 | −0.212 |
| 46 | 66 | 43°24′ | Charleston, Ore. | V/7/60 | 21–47 | 34.97 | 6.06 | 0.165 |
| 47 | 87 | 43°24′ | Charleston, Ore. | VI/1/60 | 14–66 | 33.36 | 14.37 | 0.151 |
| 48 | 108 | 44°36′ | Yaquina, Ore. | VI/3/60 | 19–61 | 31.68 | 8.02 | −0.074 |
| 50 | 45 | 46°54′ | Grays Harbor, Wash. | V/22/60 | 37–75 | 52.69 | 7.90 | −0.147 |
| 52 | 85 | 46° 0′ | Seaside, Ore. | V/21/60 | 13–65 | 26.49 | 14.73 | 0.099 |
| 53 | 75 | 41°48′ | Crescent City, Ca. | IV/3/60 | 12–54 | 29.65 | 8.30 | −0.039 |
| 54 | 86 | 40°48′ | Eureka, Ca. | IV/4/60 | 18–36 | 26.09 | 4.17 | −0.012 |
| 55 | 99 | 39°30′ | Fort Bragg, Ca. | IV/4/60 | 18–44 | 25.48 | 6.74 | −0.093 |
| 56 | 124 | 38°18′ | Bodega Bay, Ca. | IV/5/60 | 9–52 | 33.41 | 8.94 | 0.122 |
| 57 | 126 | 36°48′ | Moss Landing, Ca. | IV/16/60 | 15–55 | 30.17 | 7.02 | 0.068 |
| 58 | 81 | 43°24′ | Charleston, Ore. | XII/10/60 | 13–62 | 21.89 | 9.95 | 0.011 |
| 60 | 100 | 43°24′ | Charleston, Ore. | I/27/61 | 15–54 | 26.29 | 8.72 | −0.036 |
| 61 | 100 | 43°24′ | Charleston, Ore. | II/25/61 | 25–48 | 29.45 | 4.59 | 0.031 |
| 62 | 100 | 43°24′ | Charleston, Ore. | III/21/61 | 26–49 | 33.58 | 3.89 | 0.000 |
| 63 | 100 | 43°24′ | Charleston, Ore. | IV/25/61 | 22–56 | 44.14 | 8.20 | 0.047 |
| 64 | 99 | 43°24′ | Charleston, Ore. | V/25/61 | 24–58 | 31.59 | 6.90 | −0.095 |
| 65 | 100 | 43°24′ | Charleston, Ore. | VII/1/61 | 31–56 | 43.51 | 5.90 | 0.182 |

NOTE: The column $r_{15}$ gives the zero-order correlation coefficient relating the number of vertebrae ($_1$) to standard length ($_5$).

TABLE 1 (*Cont.*)

| FILE NUMBER | $N$ | NORTH LATITUDE | LOCALITY | DATE | STANDARD LENGTH (mm) Range | Mean | $s$ | $r_{15}$ |
|---|---|---|---|---|---|---|---|---|
| 66 | 100 | 44°36′ | Yaquina, Ore. | XI/26/60 | 11–30 | 21.23 | 4.68 | −0.085 |
| 67 | 100 | 44°36′ | Yaquina, Ore. | XII/27/60 | 16–38 | 22.94 | 5.23 | −0.074 |
| 68 | 100 | 44°36′ | Yaquina, Ore. | I/28/61 | 14–32 | 23.69 | 4.12 | 0.227 |
| 69 | 100 | 44°36′ | Yaquina, Ore. | II/26/61 | 22–45 | 27.56 | 4.67 | −0.099 |
| 70 | 100 | 44°36′ | Yaquina, Ore. | III/21/61 | 21–36 | 27.04 | 3.05 | −0.024 |
| 71 | 100 | 44°36′ | Yaquina, Ore. | IV/25/61 | 27–40 | 32.22 | 2.83 | 0.036 |
| 72 | 100 | 44°36′ | Yaquina, Ore. | V/24/61 | 19–44 | 30.37 | 6.33 | 0.141 |
| 73 | 27 | 44°36′ | Yaquina, Ore. | VI/30/61 | 46–64 | 56.19 | 4.37 | 0.305 |
| 75 | 100 | 46°54′ | Grays Harbor, Wash. | IV/23/61 | 38–65 | 49.81 | 5.74 | −0.013 |
| 77 | 100 | 46° 0′ | Seaside, Ore. | IV/24/61 | 31–76 | 52.31 | 10.21 | −0.081 |
| 78 | 61 | 41°48′ | Crescent City, Ca. | IV/8/61 | 16–51 | 32.49 | 8.58 | −0.008 |
| 79 | 86 | 40°48′ | Eureka, Ca. | IV/9/61 | 17–76 | 47.45 | 14.43 | 0.072 |
| 80 | 100 | 39°30′ | Fort Bragg, Ca. | IV/9/61 | 20–49 | 30.68 | 6.81 | 0.025 |
| 81 | 100 | 38°18′ | Bodega Bay, Ca. | IV/10/61 | 23–43 | 30.04 | 4.85 | 0.108 |
| 82 | 100 | 36°48′ | Moss Landing, Ca. | IV/10/61 | 19–52 | 28.07 | 7.81 | −0.160 |
| 83 | 100 | 43°24′ | Charleston, Ore. | I/13/62 | 16–27 | 20.54 | 2.43 | 0.110 |
| 84 | 100 | 43°24′ | Charleston, Ore. | III/21/62 | 19–32 | 24.61 | 3.24 | −0.160 |
| 85 | 100 | 43°24′ | Charleston, Ore. | V/14/62 | 19–30 | 25.55 | 2.81 | −0.097 |
| 86 | 98 | 44°36′ | Yaquina, Ore. | XII/14/61 | 14–25 | 18.70 | 2.40 | 0.012 |
| 87 | 100 | 44°36′ | Yaquina, Ore. | I/13/62 | 13–28 | 19.98 | 3.86 | −0.176 |
| 88 | 100 | 44°36′ | Yaquina, Ore. | II/11/62 | 14–25 | 20.39 | 2.26 | −0.131 |
| 89 | 100 | 44°36′ | Yaquina, Ore. | III/17/62 | 16–34 | 22.94 | 4.18 | −0.206 |
| 90 | 100 | 44°36′ | Yaquina, Ore. | IV/14/62 | 12–32 | 22.46 | 4.12 | −0.060 |
| 91 | 100 | 44°36′ | Yaquina, Ore. | V/14/62 | 18–39 | 25.49 | 4.09 | 0.002 |
| 92 | 100 | 44°36′ | Yaquina, Ore. | VI/16/62 | 14–46 | 33.73 | 6.97 | −0.081 |
| 94 | 100 | 46°54′ | Grays Harbor, Wash. | V/13/62 | 17–47 | 36.66 | 5.68 | −0.081 |
| 96 | 100 | 46° 0′ | Seaside, Ore. | V/13/62 | 19–42 | 31.16 | 5.94 | −0.162 |
| 97 | 100 | 41°48′ | Crescent City, Ca. | IV/22/62 | 12–32 | 20.13 | 3.90 | −0.162 |
| 98 | 75 | 40°48′ | Eureka, Ca. | IV/22/62 | 20–41 | 28.09 | 4.69 | −0.042 |
| 99 | 100 | 39°30′ | Fort Bragg, Ca. | IV/23/62 | 12–30 | 20.98 | 2.80 | −0.111 |
| 100 | 100 | 38°18′ | Bodega Bay, Ca. | IV/23/62 | 26–50 | 37.80 | 6.06 | 0.056 |
| 101 | 100 | 36°48′ | Moss Landing, Ca. | IV/24/62 | 16–36 | 28.28 | 3.93 | −0.246 |

in the last 2 years, probably precluded expression of the relationship in at least some cases.

### *Relationship between Meristic Character Counts and Latitude*

As a general reference, means of daily surface temperature records for two Pacific coast localities are summarized in Figure 3. Seaside, Oregon, is one of the sites visited annually, and Pacific Grove, California, located on Monterey Bay, is a few miles south of the southernmost collecting site at Moss Landing, California. These temperature records were abstracted from Scripps Institution of Oceanography (1960, 1961, 1962, 1963), Kujala and Wyatt (1961), Oliphant et al. (1962), and Still et al. (1963).

Information concerning collections used in the study of meristic character counts as a function of latitude is summarized in Table 2. The same collecting sites were used in each of the 4 years except the southernmost at Santa Cruz, California, where the San Lorenzo River habitat was destroyed by construction during the summer of 1959. Subsequent to the first year, collections were made at Moss Landing, California. Location of the collecting sites was approximated to the nearest 6′ of latitude.

TABLE 2

NUMBERS OF ELEMENTS IN THE MERISTIC CHARACTERS

| FILE NUMBER | *N* | VERTEBRAE | | | ANAL RAYS | | | DORSAL RAYS | | | DORSAL SPINES | | | *L* | *S* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range | Mean | *s* | Range | Mean | *s* | Range | Mean | *s* | Range | Mean | *s* | | |
| 1 | 100 | 37–38 | 37.50 | 0.50 | 16–19 | 17.49 | 0.58 | 17–20 | 18.48 | 0.56 | 7–9 | 7.39 | 0.51 | | * |
| 2 | 97 | 37–38 | 37.57 | 0.50 | 16–19 | 17.55 | 0.60 | 17–20 | 18.43 | 0.56 | 7–8 | 7.23 | 0.42 | | * |
| 3 | 64 | 36–38 | 37.50 | 0.53 | 16–19 | 17.44 | 0.61 | 17–20 | 18.50 | 0.59 | 7–9 | 7.38 | 0.52 | | * |
| 4 | 92 | 36–39 | 37.62 | 0.53 | 15–19 | 17.64 | 0.62 | 15–20 | 18.47 | 0.67 | 7–8 | 7.32 | 0.47 | | * |
| 5 | 209 | 36–39 | 37.42 | 0.52 | 16–19 | 17.53 | 0.58 | 17–20 | 18.56 | 0.59 | 6–9 | 7.33 | 0.50 | | * |
| 6 | 158 | 36–38 | 37.51 | 0.51 | 16–19 | 17.65 | 0.54 | 17–20 | 18.54 | 0.57 | 6–8 | 7.29 | 0.47 | | * |
| 9 | 621 | 36–39 | 37.59 | 0.54 | 15–19 | 17.69 | 0.57 | 17–21 | 18.53 | 0.58 | 6–9 | 7.39 | 0.52 | | * |
| 10 | 493 | 36–39 | 37.61 | 0.54 | 15–20 | 17.70 | 0.61 | 17–20 | 18.59 | 0.58 | 6–9 | 7.40 | 0.53 | | * |
| 12 | 177 | 37–39 | 37.80 | 0.61 | 16–19 | 17.86 | 0.62 | 18–21 | 18.75 | 0.65 | 6–8 | 7.37 | 0.52 | * | |
| 14 | 244 | 36–39 | 37.66 | 0.55 | 17–19 | 17.83 | 0.55 | 17–20 | 18.60 | 0.59 | 6–8 | 7.34 | 0.49 | * | |
| 15 | 276 | 36–39 | 37.58 | 0.54 | 16–19 | 17.66 | 0.58 | 16–21 | 18.59 | 0.62 | 6–9 | 7.37 | 0.51 | * | |
| 16 | 107 | 36–38 | 37.42 | 0.53 | 16–19 | 17.46 | 0.65 | 17–20 | 18.42 | 0.63 | 6–8 | 7.32 | 0.49 | * | |
| 17 | 85 | 36–38 | 37.15 | 0.52 | 16–19 | 17.11 | 0.66 | 17–20 | 18.26 | 0.58 | 6–9 | 7.25 | 0.49 | * | |
| 18 | 314 | 36–39 | 37.19 | 0.56 | 15–18 | 17.11 | 0.65 | 17–20 | 18.11 | 0.58 | 6–8 | 7.26 | 0.47 | * | |
| 19 | 215 | 36–38 | 37.01 | 0.48 | 16–19 | 17.11 | 0.57 | 17–19 | 18.07 | 0.52 | 6–9 | 7.23 | 0.48 | * | |
| 20 | 423 | 36–39 | 37.64 | 0.56 | 16–19 | 17.86 | 0.58 | 17–20 | 18.66 | 0.57 | 7–9 | 7.46 | 0.52 | * | * |
| 21 | 311 | 37–39 | 37.62 | 0.51 | 16–19 | 17.86 | 0.52 | 17–21 | 18.67 | 0.56 | 6–8 | 7.38 | 0.50 | * | * |
| 22 | 184 | 37–39 | 37.70 | 0.52 | 16–20 | 17.88 | 0.56 | 17–20 | 18.76 | 0.54 | 6–9 | 7.43 | 0.54 | | * |
| 23 | 226 | 36–39 | 37.62 | 0.57 | 16–19 | 17.81 | 0.57 | 17–20 | 18.68 | 0.59 | 6–8 | 7.35 | 0.50 | | * |
| 31 | 104 | 36–39 | 37.51 | 0.54 | 17–19 | 17.85 | 0.50 | 18–20 | 18.73 | 0.54 | 7–8 | 7.33 | 0.47 | | * |
| 32 | 44 | 37–39 | 37.68 | 0.60 | 17–19 | 17.89 | 0.54 | 18–20 | 18.70 | 0.51 | 7–8 | 7.36 | 0.49 | | * |
| 34 | 51 | 36–39 | 37.63 | 0.63 | 16–19 | 17.67 | 0.62 | 18–20 | 18.63 | 0.60 | 7–8 | 7.35 | 0.48 | | * |
| 36 | 114 | 37–40 | 37.58 | 0.56 | 16–19 | 17.35 | 0.53 | 17–20 | 18.30 | 0.66 | 6–8 | 7.25 | 0.45 | | * |
| 37 | 120 | 37–40 | 37.56 | 0.55 | 16–19 | 17.36 | 0.59 | 16–19 | 18.28 | 0.57 | 6–9 | 7.29 | 0.52 | | * |
| 38 | 57 | 36–38 | 37.46 | 0.54 | 16–18 | 17.35 | 0.58 | 17–19 | 18.33 | 0.61 | 7–8 | 7.23 | 0.42 | | * |
| 39 | 97 | 37–39 | 37.51 | 0.52 | 16–19 | 17.39 | 0.57 | 17–20 | 18.36 | 0.56 | 7–9 | 7.30 | 0.48 | | * |
| 40 | 54 | 36–38 | 37.50 | 0.54 | 16–19 | 17.48 | 0.57 | 17–20 | 18.44 | 0.72 | 6–8 | 7.20 | 0.56 | | * |
| 41 | 212 | 36–39 | 37.79 | 0.49 | 16–19 | 17.71 | 0.55 | 17–20 | 18.59 | 0.56 | 6–9 | 7.26 | 0.49 | | * |
| 42 | 111 | 36–39 | 37.68 | 0.53 | 17–19 | 17.74 | 0.50 | 17–20 | 18.59 | 0.61 | 7–9 | 7.44 | 0.52 | | * |
| 43 | 110 | 36–39 | 37.68 | 0.53 | 14–19 | 17.75 | 0.67 | 17–20 | 18.59 | 0.58 | 7–8 | 7.33 | 0.47 | | * |
| 44 | 114 | 37–39 | 37.70 | 0.55 | 16–19 | 17.66 | 0.62 | 17–20 | 18.55 | 0.65 | 7–8 | 7.32 | 0.47 | | * |
| 45 | 95 | 36–39 | 37.81 | 0.51 | 16–19 | 17.74 | 0.59 | 17–20 | 18.62 | 0.60 | 7–8 | 7.35 | 0.48 | * | * |
| 46 | 66 | 37–39 | 37.73 | 0.48 | 17–19 | 17.88 | 0.48 | 18–20 | 18.65 | 0.62 | 5–8 | 7.24 | 0.53 | * | * |
| 47 | 87 | 36–39 | 37.59 | 0.56 | 16–19 | 17.69 | 0.65 | 17–20 | 18.49 | 0.59 | 6–8 | 7.31 | 0.54 | | * |
| 48 | 108 | 37–39 | 37.75 | 0.51 | 16–19 | 17.82 | 0.54 | 18–20 | 18.73 | 0.61 | 7–8 | 7.43 | 0.50 | | * |
| 50 | 45 | 37–39 | 37.82 | 0.44 | 17–19 | 17.80 | 0.50 | 17–20 | 18.53 | 0.66 | 6–8 | 7.40 | 0.54 | * | |
| 52 | 85 | 37–39 | 37.69 | 0.54 | 16–19 | 17.76 | 0.59 | 18–20 | 18.65 | 0.50 | 6–9 | 7.44 | 0.54 | * | |
| 53 | 75 | 36–38 | 37.44 | 0.53 | 17–19 | 17.60 | 0.52 | 17–19 | 18.37 | 0.59 | 7–8 | 7.56 | 0.50 | * | |
| 54 | 86 | 36–38 | 37.29 | 0.55 | 16–19 | 17.21 | 0.58 | 17–19 | 18.19 | 0.56 | 5–8 | 7.35 | 0.55 | * | |
| 55 | 99 | 36–38 | 37.28 | 0.50 | 16–19 | 17.16 | 0.68 | 16–19 | 18.27 | 0.59 | 7–8 | 7.40 | 0.49 | * | |
| 56 | 124 | 36–38 | 37.24 | 0.55 | 16–18 | 17.17 | 0.61 | 17–19 | 18.12 | 0.59 | 6–8 | 7.46 | 0.52 | * | |
| 57 | 126 | 35–38 | 36.57 | 0.72 | 15–18 | 16.69 | 0.65 | 16–19 | 17.65 | 0.76 | 6–8 | 7.13 | 0.49 | * | |
| 58 | 81 | 36–39 | 37.67 | 0.55 | 17–19 | 17.70 | 0.58 | 17–20 | 18.47 | 0.61 | 7–8 | 7.32 | 0.47 | | * |
| 60 | 100 | 36–38 | 37.59 | 0.51 | 16–19 | 17.61 | 0.57 | 17–20 | 18.51 | 0.56 | 6–8 | 7.35 | 0.50 | | * |
| 61 | 100 | 37–38 | 37.60 | 0.49 | 16–19 | 17.68 | 0.58 | 16–20 | 18.52 | 0.63 | 7–8 | 7.38 | 0.49 | | * |
| 62 | 100 | 37–39 | 37.62 | 0.53 | 16–19 | 17.74 | 0.52 | 18–20 | 18.55 | 0.57 | 6–8 | 7.32 | 0.51 | | * |
| 63 | 100 | 36–39 | 37.63 | 0.58 | 17–19 | 17.71 | 0.54 | 18–20 | 18.51 | 0.52 | 6–8 | 7.29 | 0.48 | * | * |
| 64 | 99 | 36–39 | 37.71 | 0.54 | 16–19 | 17.83 | 0.50 | 18–20 | 18.75 | 0.48 | 6–8 | 7.42 | 0.52 | | * |
| 65 | 100 | 36–39 | 37.69 | 0.55 | 16–19 | 17.78 | 0.58 | 18–20 | 18.81 | 0.54 | 7–8 | 7.32 | 0.47 | | * |

NOTE: In column *L*, * indicates use of data in the latitudinal study. In column *S*, * indicates use of data in the seasonal study of either the Charleston or the Yaquina, Oregon, population.

TABLE 2 (*Cont.*)

| FILE NUMBER | *N* | VERTEBRAE Range | Mean | *s* | ANAL RAYS Range | Mean | *s* | DORSAL RAYS Range | Mean | *s* | DORSAL SPINES Range | Mean | *s* | *L* | *S* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 66 | 100 | 37–39 | 37.56 | 0.56 | 16–18 | 17.39 | 0.51 | 17–19 | 18.25 | 0.54 | 6–8 | 7.35 | 0.52 | | * |
| 67 | 100 | 37–39 | 37.57 | 0.54 | 17–20 | 17.60 | 0.59 | 16–20 | 18.29 | 0.59 | 7–8 | 7.32 | 0.47 | | * |
| 68 | 100 | 35–38 | 37.51 | 0.56 | 16–18 | 17.45 | 0.63 | 17–20 | 18.35 | 0.63 | 6–8 | 7.24 | 0.45 | | * |
| 69 | 100 | 36–38 | 37.48 | 0.52 | 16–18 | 17.51 | 0.56 | 17–19 | 18.46 | 0.54 | 7–8 | 7.23 | 0.42 | | * |
| 70 | 100 | 36–39 | 37.58 | 0.59 | 16–19 | 17.64 | 0.60 | 17–20 | 18.56 | 0.62 | 6–8 | 7.37 | 0.51 | | * |
| 71 | 100 | 37–39 | 37.73 | 0.49 | 17–19 | 17.81 | 0.54 | 17–20 | 18.62 | 0.58 | 7–8 | 7.41 | 0.49 | * | * |
| 72 | 100 | 37–39 | 37.77 | 0.47 | 17–19 | 17.94 | 0.55 | 17–20 | 18.74 | 0.56 | 7–8 | 7.39 | 0.49 | | * |
| 73 | 27 | 37–38 | 37.66 | 0.48 | 17–19 | 17.67 | 0.62 | 18–19 | 18.33 | 0.48 | 7–8 | 7.22 | 0.42 | | * |
| 75 | 100 | 37–39 | 37.86 | 0.49 | 16–19 | 17.83 | 0.55 | 17–20 | 18.66 | 0.59 | 7–8 | 7.35 | 0.48 | * | |
| 77 | 100 | 37–39 | 37.63 | 0.54 | 16–19 | 17.77 | 0.55 | 17–21 | 18.58 | 0.64 | 7–9 | 7.44 | 0.52 | * | |
| 78 | 61 | 35–39 | 37.52 | 0.67 | 15–20 | 17.56 | 0.76 | 17–20 | 18.39 | 0.56 | 6–8 | 7.30 | 0.49 | * | |
| 79 | 86 | 36–38 | 37.56 | 0.52 | 16–19 | 17.65 | 0.61 | 17–20 | 18.37 | 0.60 | 7–8 | 7.29 | 0.46 | * | |
| 80 | 100 | 36–39 | 37.47 | 0.54 | 16–19 | 17.36 | 0.63 | 17–20 | 18.26 | 0.56 | 7–9 | 7.34 | 0.50 | * | |
| 81 | 100 | 36–38 | 37.38 | 0.53 | 16–18 | 17.17 | 0.62 | 16–20 | 18.21 | 0.62 | 6–8 | 7.24 | 0.49 | * | |
| 82 | 100 | 35–39 | 36.64 | 0.75 | 15–18 | 16.60 | 0.71 | 15–19 | 17.56 | 0.87 | 6–8 | 7.22 | 0.48 | * | |
| 83 | 100 | 37–39 | 37.58 | 0.52 | 16–19 | 17.53 | 0.59 | 17–19 | 18.48 | 0.52 | 6–8 | 7.37 | 0.51 | | * |
| 84 | 100 | 36–38 | 37.77 | 0.45 | 16–20 | 17.85 | 0.54 | 17–20 | 18.66 | 0.59 | 7–8 | 7.30 | 0.46 | | * |
| 85 | 100 | 37–39 | 37.84 | 0.49 | 17–19 | 17.98 | 0.45 | 18–19 | 18.73 | 0.45 | 7–8 | 7.45 | 0.50 | * | * |
| 86 | 98 | 36–39 | 37.57 | 0.56 | 16–19 | 17.53 | 0.58 | 17–20 | 18.39 | 0.55 | 7–9 | 7.40 | 0.53 | | * |
| 87 | 100 | 36–39 | 37.63 | 0.56 | 16–19 | 17.65 | 0.58 | 17–19 | 18.47 | 0.54 | 7–9 | 7.35 | 0.50 | | * |
| 88 | 100 | 37–39 | 37.65 | 0.56 | 17–19 | 17.69 | 0.54 | 17–20 | 18.54 | 0.58 | 7–8 | 7.28 | 0.45 | | * |
| 89 | 100 | 37–39 | 37.83 | 0.49 | 17–20 | 17.88 | 0.54 | 18–20 | 18.73 | 0.55 | 6–8 | 7.34 | 0.50 | | * |
| 90 | 100 | 36–39 | 37.78 | 0.52 | 17–19 | 18.00 | 0.53 | 18–20 | 18.78 | 0.52 | 6–8 | 7.42 | 0.52 | | * |
| 91 | 100 | 37–39 | 37.81 | 0.47 | 17–19 | 17.88 | 0.52 | 17–20 | 18.71 | 0.54 | 7–8 | 7.34 | 0.48 | * | * |
| 92 | 100 | 36–39 | 37.68 | 0.57 | 16–19 | 18.84 | 0.58 | 18–20 | 18.65 | 0.59 | 7–8 | 7.31 | 0.46 | | * |
| 94 | 100 | 37–39 | 37.88 | 0.57 | 16–19 | 17.97 | 0.61 | 17–20 | 18.82 | 0.59 | 7–8 | 7.36 | 0.48 | * | |
| 96 | 100 | 36–39 | 37.77 | 0.55 | 15–19 | 17.92 | 0.61 | 17–20 | 18.70 | 0.59 | 6–8 | 7.29 | 0.48 | * | |
| 97 | 100 | 37–39 | 37.65 | 0.52 | 17–19 | 17.75 | 0.56 | 17–20 | 18.56 | 0.62 | 7–8 | 7.27 | 0.45 | * | |
| 98 | 75 | 37–39 | 37.55 | 0.53 | 16–19 | 17.63 | 0.56 | 17–19 | 18.45 | 0.60 | 7–8 | 7.39 | 0.49 | * | |
| 99 | 100 | 36–38 | 37.33 | 0.53 | 16–19 | 17.42 | 0.64 | 17–19 | 18.22 | 0.54 | 5–8 | 7.32 | 0.55 | * | |
| 100 | 100 | 36–38 | 37.29 | 0.56 | 16–18 | 17.17 | 0.64 | 17–19 | 18.12 | 0.52 | 6–8 | 7.31 | 0.53 | * | |
| 101 | 100 | 35–38 | 36.34 | 0.59 | 15–18 | 16.56 | 0.67 | 16–19 | 17.31 | 0.69 | 6–8 | 7.07 | 0.38 | * | |

Conditions of the meristic characters in the latitude study appear in Table 2 and Figures 1 and 2. Figure 1 shows two well-defined breaks, one in the vicinity of 42 to 43° N, and the other between the two southernmost stations. Figure 1 shows that at a given station there are occasional significant differences between counts of different years. However, these are exceptional. Examination of Figure 3 indicates that such differences can, in some cases, be related to year to year differences in developmental temperatures. Within given years, in general, the collections from Charleston, Oregon (43°24′ N), do not differ from their counterparts from the three stations to the north. Habitats are numerous and populations are large throughout the range covered by the four northern stations. In the aggregate, the four northern stations show many more similarities than differences.

Large estuarine habitats become fewer in number and more widely separated as one moves south from about 43° N. South of this latitude the cline in conditions manifests itself. Plots of numbers of anal and dorsal rays as a function of latitude are similar to the vertebral data that appear in Figure 1.

Figure 2 shows that the number of dorsal spines has little relationship to latitude. However, in comparing the two stations at the

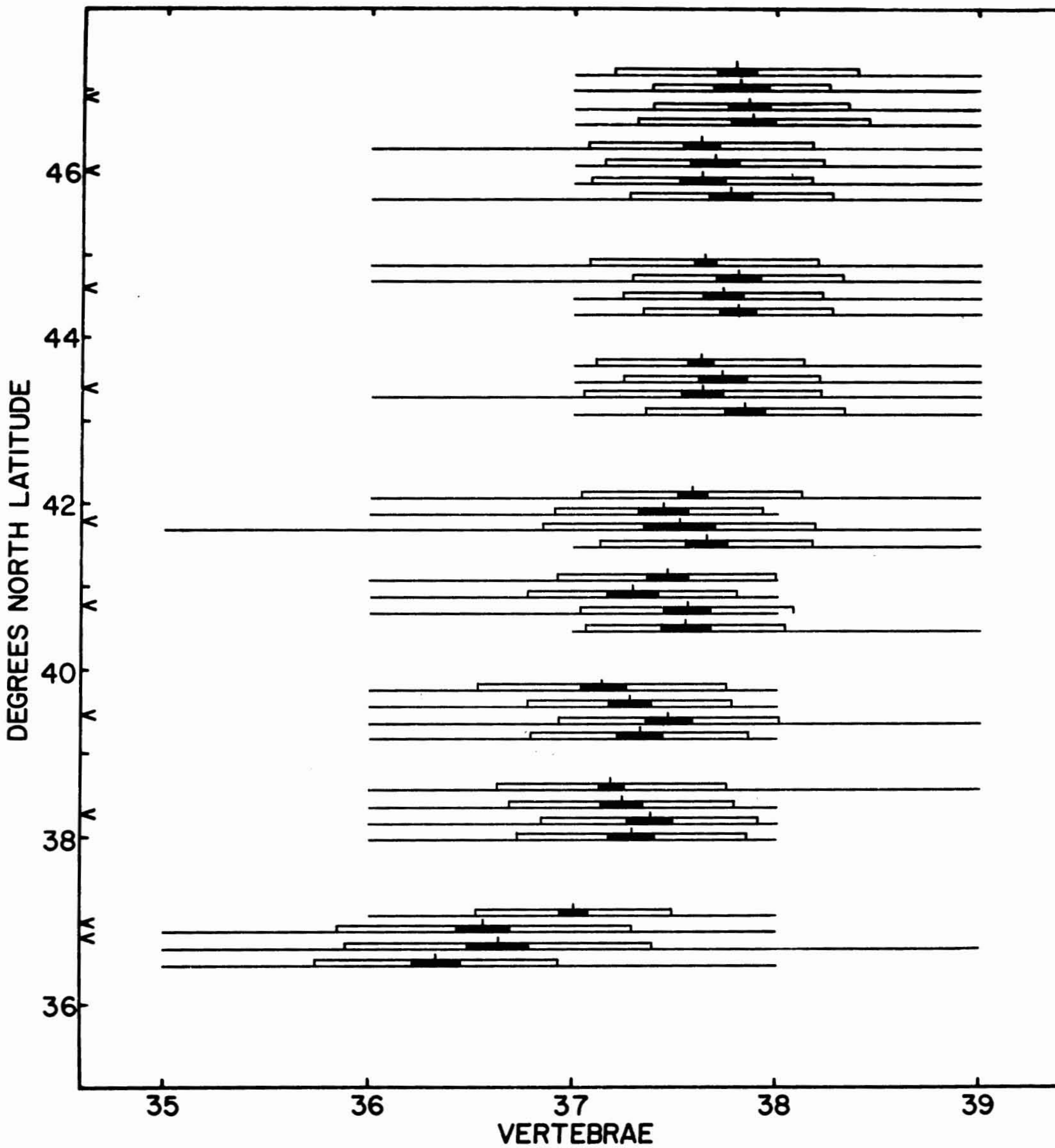


FIGURE 1. The relationship between latitude and vertebral number. Markers on the ordinate indicate latitudes of collecting sites. For each site the data occupy four positions designated from the top, study years 1, 2, 3, and 4. The same format is followed in Figure 2.

extremes of the range under study, condition of the dorsal spines is significantly different in 2 of the 4 years. Evidence has not been found to indicate that the number of spines in the dorsal fin is susceptible to developmental temperature.

When the numbers of vertebrae, dorsal rays, and anal rays representing the two extreme stations are compared, a few cases are found in given years in which the coefficient of difference $[CD = (\overline{x}_1 - \overline{x}_2)/(s_1 + s_2)]$ approaches the conventional level (1.28) for

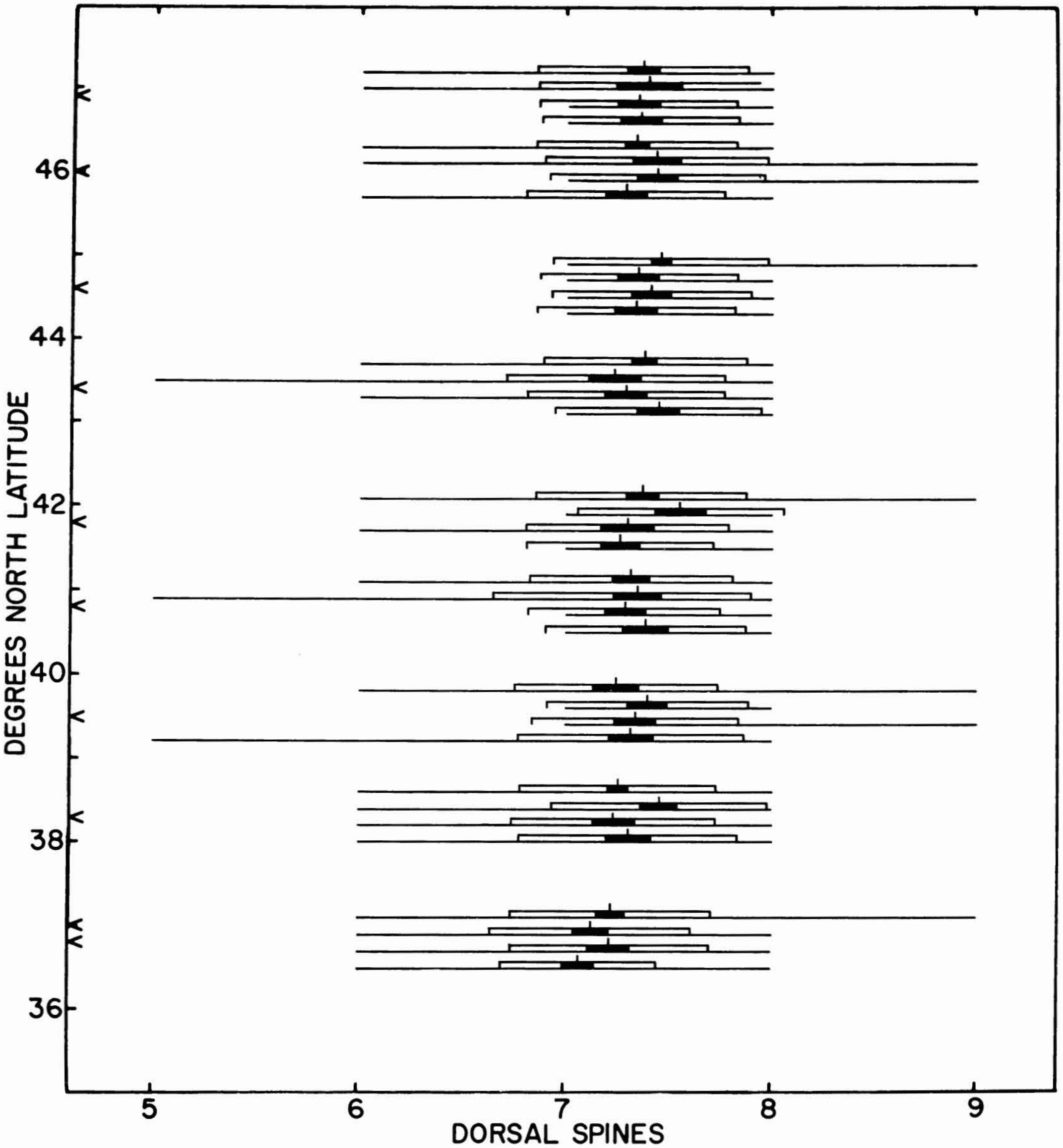


FIGURE 2. The relationship between latitude and number of dorsal spines. See explanation, caption of Figure 1.

delineation of subspecies accepted by Mayr (1963).

In a few instances the variation of a given character is conspicuously greater among the fish collected at the southernmost station than at the other sites; see collections 57 and 82 listed in Table 2. Otherwise, the degree of variation is remarkably consistent.

*Seasonal Effects on Meristic Character Counts*

Collections used in the study of seasonal effects on meristic character counts are identified in Table 2 and two representative sets of data are shown in Figures 4 and 5. Generally speaking, vertebral counts among the April or May arrivals are higher than the

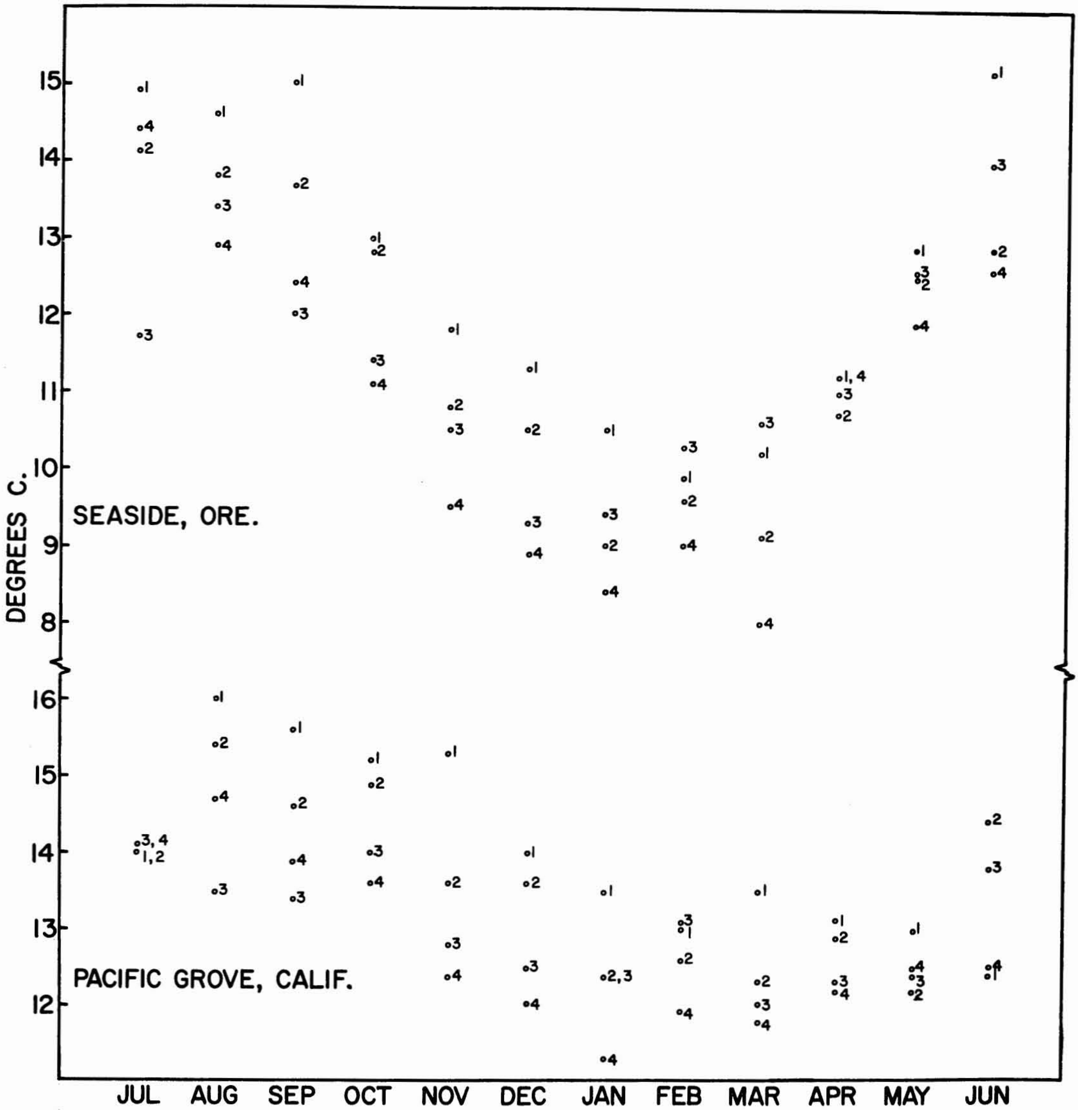


FIGURE 3. Monthly means of surface temperatures at two representative collecting sites. Each point is identified as to study year as follows: 1, 1958–1959; 2, 1959–1960; 3, 1960–1961; 4, 1961–1962. Datum points for Pacific Grove, California are from Scripps Institution of Oceanography surface water temperatures at shore stations, U.S. west coast and Baja California; Seaside, Oregon datum points are from: years 1 and 2, Kujala and Wyatt (1961); year 3, Oliphant et al. (1962); year 4, Still et al. (1963).

counts of fish that arrived during December or January. These findings are reasonable since the early arrivals could be expected to have passed their phenocritical periods during higher temperatures of late summer and autumn; those arriving in the spring would have passed such periods during the lower temperatures of winter. The changes from month to month and year to year are orderly, and significant differences in these comparisons are exceptions to the rule.

Month to month changes in meristic character counts indicate that animals arriving from the plankton in February and March may have passed their phenocritical periods during temperature transitions. It seems that

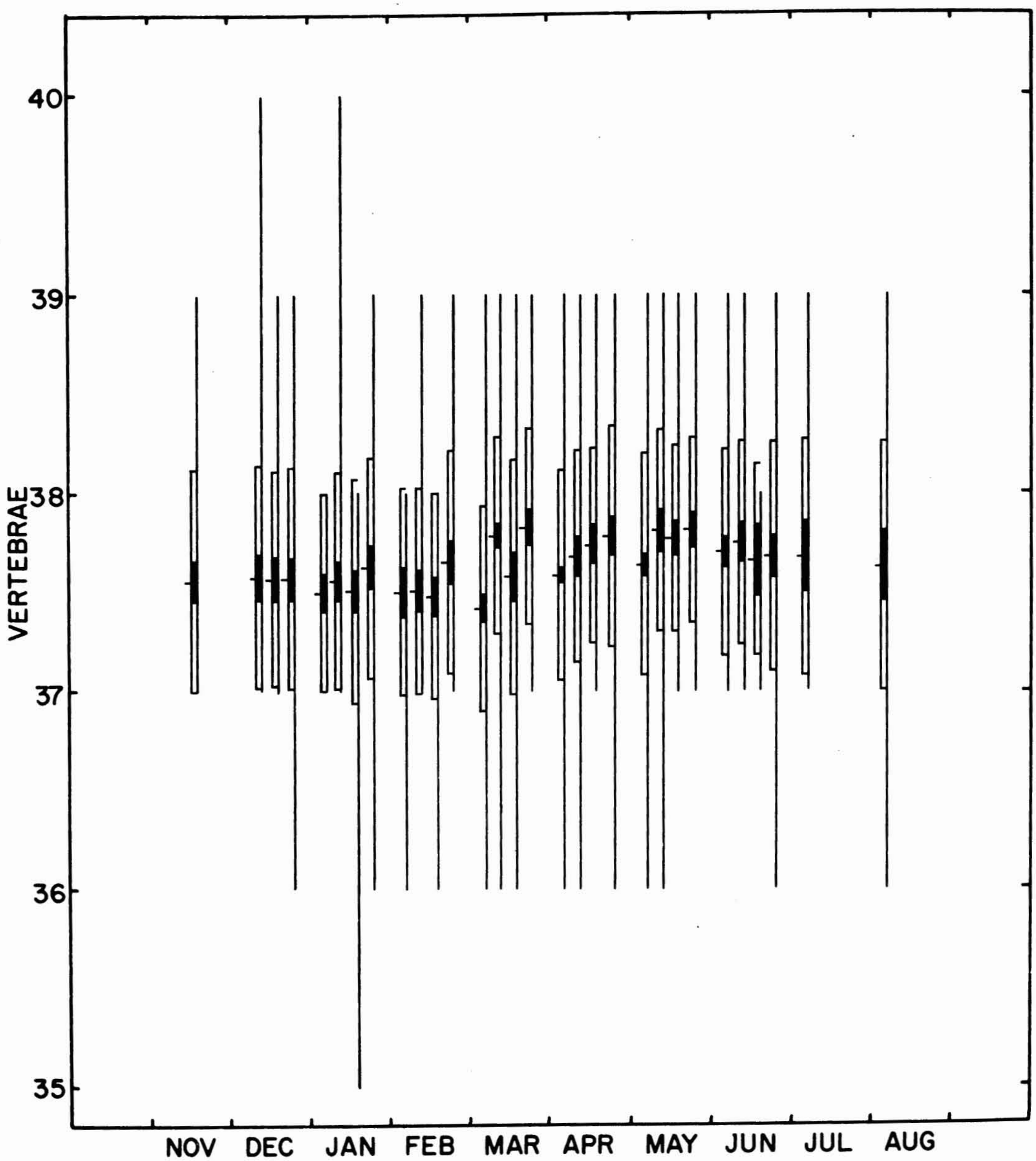


FIGURE 4. The relationship between season and number of vertebrae in fish taken at the Yaquina, Oregon, collecting site. For each month shown on the graph, there are four available positions. From left to right, these positions represent study years 1, 2, 3, and 4. (For example, collections were made in all years in January but only in the third year in November.) The same format is followed in Figure 5.

such a transition would result in a greater degree of variation in a given character. However, the degree of variation seen among these collections is comparable to that in collections taken at other times.

Plots of data on anal and dorsal rays from the Yaquina, Oregon, station and comparable plots of data from the Charleston, Oregon, station show seasonal patterns similar to those of the vertebral data in Figure 4. As Figure 5 indicates, seasonal trends are not evident in dorsal spine counts.

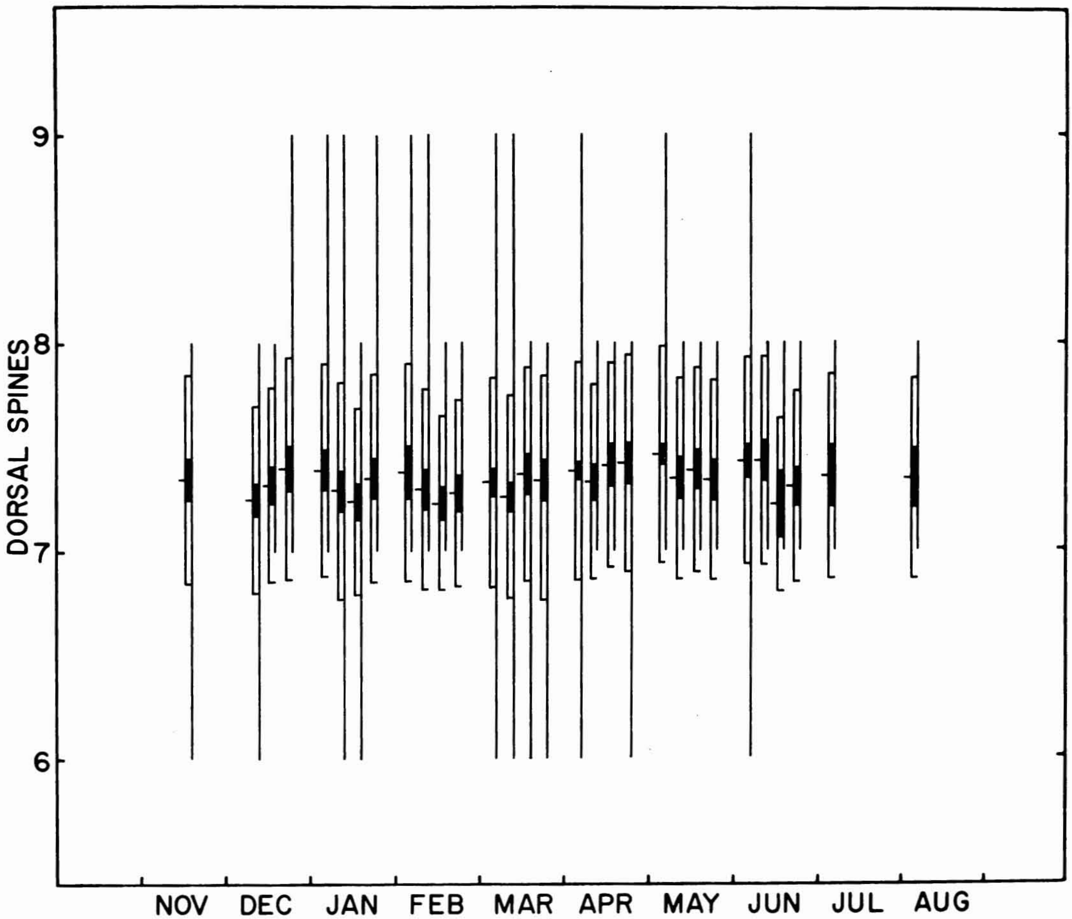


FIGURE 5. The relationship between season and number of dorsal spines in fish taken at the Yaquina, Oregon, collecting site. See explanation, caption of Figure 4.

*Relationships among Meristic Characters*

The zero-order correlation coefficients listed in Table 3 show that in about 75 percent of the collections taken there is a highly significant relationship between number of vertebrae and number of rays in either of the soft fins. The coefficient $r_{14}$ shows a significant relationship between vertebrae and dorsal spines in 18 of the 81 collections. This is a much greater number than would be expected due to chance alone. In almost 90 percent of the collections, the coefficient $r_{23}$ is highly significant, showing an intimate relationship between the anal and soft dorsal fins. The coefficients $r_{24}$ and $r_{34}$ indicate little relationship between number of spines and rays in either the anal or the dorsal fin. Note that all the statistically significant coefficients are positive.

As would be expected from the coefficients in Table 3, the summary of first-order partial correlation coefficients in Table 4 indicates the condition of the spinous dorsal has little or no effect on the affinities the other three characters show for one another.

Table 4 also summarizes the number of second-order partial correlation coefficients found to be significant. Here we see that the strong relationship the two soft fins show for

TABLE 3

ZERO-ORDER CORRELATION COEFFICIENTS INDICATING TOTAL CORRELATION BETWEEN PAIRS OF CHARACTERS

| FILE NUMBER | $N$ | CRITICAL $r\,(+\,-)$ | $r_{12}$ | $r_{13}$ | $r_{14}$ | $r_{23}$ | $r_{24}$ | $r_{34}$ |
|---|---|---|---|---|---|---|---|---|
| 1 | 100 | 0.257 | 0.296* | 0.288* | 0.256 | 0.297* | −0.004 | 0.152 |
| 2 | 97 | 0.260 | 0.491* | 0.307* | 0.125 | 0.441* | 0.082 | 0.066 |
| 3 | 64 | 0.320 | 0.484* | 0.251 | −0.114 | 0.525* | 0.174 | 0.103 |
| 4 | 92 | 0.267 | 0.481* | 0.443* | 0.090 | 0.433* | 0.242 | 0.121 |
| 5 | 209 | 0.178 | 0.265* | 0.333* | 0.083 | 0.466* | −0.014 | 0.068 |
| 6 | 158 | 0.204 | 0.373* | 0.434* | 0.090 | 0.473* | 0.025 | 0.023 |
| 9 | 621 | 0.103 | 0.301* | 0.349* | 0.153* | 0.404* | 0.071 | 0.100 |
| 10 | 493 | 0.116 | 0.372* | 0.341* | 0.168* | 0.401* | 0.113 | 0.070 |
| 12 | 177 | 0.193 | 0.397* | 0.488* | 0.161 | 0.495* | 0.035 | 0.124 |
| 14 | 244 | 0.165 | 0.388* | 0.358* | 0.105 | 0.508* | 0.155 | 0.156 |
| 15 | 276 | 0.155 | 0.275* | 0.371* | 0.260* | 0.350* | 0.102 | 0.145 |
| 16 | 107 | 0.248 | 0.367* | 0.397* | 0.243 | 0.633* | 0.043 | 0.175 |
| 17 | 85 | 0.278 | 0.507* | 0.338* | 0.244 | 0.334* | 0.141 | 0.024 |
| 18 | 314 | 0.145 | 0.261* | 0.428* | 0.219* | 0.500* | 0.089 | 0.167* |
| 19 | 215 | 0.175 | 0.305* | 0.392* | 0.231* | 0.377* | 0.116 | 0.165 |
| 20 | 423 | 0.125 | 0.296* | 0.408* | 0.170* | 0.456* | 0.103 | 0.113 |
| 21 | 311 | 0.146 | 0.366* | 0.357* | 0.162* | 0.428* | 0.120 | 0.020 |
| 22 | 184 | 0.189 | 0.323* | 0.234* | 0.229* | 0.350* | 0.070 | 0.111 |
| 23 | 226 | 0.171 | 0.341* | 0.378* | 0.124 | 0.363* | 0.039 | −0.042 |
| 31 | 104 | 0.252 | 0.181 | 0.308* | 0.217 | 0.276* | 0.051 | −0.032 |
| 32 | 44 | 0.384 | 0.389* | 0.445* | 0.166 | 0.554* | 0.340 | 0.256 |
| 34 | 51 | 0.358 | 0.492* | 0.578* | 0.243 | 0.573* | 0.067 | 0.118 |
| 36 | 114 | 0.240 | 0.321* | 0.340* | 0.271* | 0.428* | 0.190 | 0.284* |
| 37 | 120 | 0.234 | 0.389* | 0.326* | 0.306* | 0.371* | 0.040 | −0.026 |
| 38 | 57 | 0.339 | 0.564* | 0.292 | 0.241 | 0.673* | 0.322 | 0.255 |
| 39 | 97 | 0.260 | 0.343* | 0.438* | 0.262* | 0.627* | 0.176 | 0.097 |
| 40 | 54 | 0.348 | 0.425* | 0.437* | 0.341 | 0.706* | 0.333 | 0.332 |
| 41 | 212 | 0.177 | 0.337* | 0.381* | 0.228* | 0.380* | 0.147 | 0.114 |
| 42 | 111 | 0.244 | 0.576* | 0.429* | 0.264* | 0.656* | 0.169 | 0.268* |
| 43 | 110 | 0.245 | 0.253* | 0.333* | 0.146 | 0.415* | 0.121 | 0.293* |
| 44 | 114 | 0.240 | 0.218 | 0.391* | −0.033 | 0.492* | −0.041 | −0.013 |
| 45 | 95 | 0.263 | 0.540* | 0.385* | 0.185 | 0.405* | 0.140 | 0.202 |
| 46 | 66 | 0.315 | 0.452* | 0.192 | 0.324* | 0.321* | 0.360* | 0.121 |
| 47 | 87 | 0.275 | 0.090 | 0.345* | 0.240 | 0.435* | 0.213 | −0.013 |
| 48 | 108 | 0.247 | 0.343* | 0.263* | 0.055 | 0.451* | 0.072 | 0.197 |
| 50 | 45 | 0.380 | 0.041 | 0.099 | 0.019 | 0.191 | −0.033 | −0.229 |
| 52 | 85 | 0.278 | −0.155 | 0.257 | 0.013 | 0.197 | 0.248 | 0.089 |
| 53 | 75 | 0.296 | 0.257 | 0.379* | 0.130 | 0.363* | −0.114 | −0.123 |
| 54 | 86 | 0.276 | 0.325* | 0.354* | 0.050 | 0.349* | 0.176 | 0.092 |
| 55 | 99 | 0.258 | 0.256 | 0.189 | 0.083 | 0.579* | 0.113 | 0.261* |
| 56 | 124 | 0.231 | 0.017 | 0.310* | 0.207 | 0.366* | 0.100 | 0.056 |
| 57 | 126 | 0.229 | 0.466* | 0.571* | 0.088 | 0.667* | 0.049 | 0.163 |
| 58 | 81 | 0.285 | 0.354* | 0.471* | 0.032 | 0.676* | 0.170 | 0.122 |
| 60 | 100 | 0.257 | 0.418* | 0.419* | −0.104 | 0.474* | 0.023 | 0.006 |
| 61 | 100 | 0.257 | 0.430* | 0.321* | 0.135 | 0.459* | 0.147 | 0.239 |
| 62 | 100 | 0.257 | 0.187 | 0.198 | 0.081 | 0.211 | 0.050 | 0.048 |
| 63 | 100 | 0.257 | 0.075 | 0.229 | 0.100 | 0.244 | 0.174 | 0.171 |
| 64 | 99 | 0.258 | 0.041 | 0.145 | 0.084 | 0.244 | 0.128 | 0.148 |
| 65 | 100 | 0.257 | 0.294* | 0.378* | 0.036 | 0.475* | 0.002 | 0.201 |

NOTE: Critical value of $r$ shown with $N$-2 d.f. and $P = 0.01$. Subscript 1, vertebrae; 2, anal rays; 3, dorsal rays; 4, dorsal spines; *, denotes statistical significance.

TABLE 3 (*Cont.*)

| FILE NUMBER | $N$ | CRITICAL $r\,(+\,-)$ | $r_{12}$ | $r_{13}$ | $r_{14}$ | $r_{23}$ | $r_{24}$ | $r_{34}$ |
|---|---|---|---|---|---|---|---|---|
| 66 | 100 | 0.257 | 0.255 | 0.135 | 0.160 | 0.450* | 0.133 | 0.234 |
| 67 | 100 | 0.257 | 0.507* | 0.207 | 0.111 | 0.251 | 0.176 | 0.063 |
| 68 | 100 | 0.257 | 0.348* | 0.323* | 0.150 | 0.497* | 0.043 | 0.129 |
| 69 | 100 | 0.257 | 0.365* | 0.320* | −0.048 | 0.252 | 0.012 | −0.026 |
| 70 | 100 | 0.257 | 0.229 | 0.180 | 0.324* | 0.466* | 0.212 | 0.137 |
| 71 | 100 | 0.257 | 0.449* | 0.345* | 0.170 | 0.407* | −0.008 | 0.020 |
| 72 | 100 | 0.257 | 0.458* | 0.348* | −0.045 | 0.376* | 0.051 | −0.068 |
| 73 | 27 | 0.487 | 0.129 | 0.167 | 0.378 | 0.387 | 0.146 | 0.189 |
| 75 | 100 | 0.257 | 0.135 | 0.287* | 0.124 | 0.442* | −0.078 | −0.003 |
| 77 | 100 | 0.257 | 0.288* | 0.305* | 0.225 | 0.472* | 0.111 | 0.137 |
| 78 | 61 | 0.327 | 0.491* | 0.463* | 0.228 | 0.377* | 0.219 | 0.238 |
| 79 | 86 | 0.276 | 0.323* | 0.308* | 0.199 | 0.330* | 0.157 | 0.074 |
| 80 | 100 | 0.257 | 0.181 | 0.360* | 0.114 | 0.419* | −0.040 | −0.103 |
| 81 | 100 | 0.257 | 0.109 | 0.211 | 0.112 | 0.342* | −0.003 | 0.158 |
| 82 | 100 | 0.257 | 0.545* | 0.533* | 0.306* | 0.596* | 0.112 | 0.065 |
| 83 | 100 | 0.257 | 0.340* | 0.457* | 0.253 | 0.475* | 0.249 | 0.354* |
| 84 | 100 | 0.257 | 0.527* | 0.429* | 0.241 | 0.442* | 0.142 | 0.193 |
| 85 | 100 | 0.257 | 0.216 | 0.264* | 0.257* | 0.427* | 0.221 | 0.188 |
| 86 | 98 | 0.259 | 0.394* | 0.281* | 0.060 | 0.547* | 0.044 | 0.031 |
| 87 | 100 | 0.257 | 0.314* | 0.280* | 0.178 | 0.502* | 0.079 | 0.095 |
| 88 | 100 | 0.257 | 0.239 | 0.276* | 0.072 | 0.249 | 0.028 | −0.005 |
| 89 | 100 | 0.257 | 0.267* | 0.240 | 0.279* | 0.404* | 0.117 | 0.341* |
| 90 | 100 | 0.257 | 0.362* | 0.412* | 0.046 | 0.508* | −0.037 | 0.121 |
| 91 | 100 | 0.257 | 0.325* | 0.343* | 0.158 | 0.418* | 0.085 | 0.113 |
| 92 | 100 | 0.257 | 0.305* | 0.235 | 0.074 | 0.452* | 0.185 | 0.178 |
| 94 | 100 | 0.257 | 0.279* | 0.412* | 0.048 | 0.320* | 0.071 | 0.194 |
| 96 | 100 | 0.257 | 0.246 | 0.345* | 0.180 | 0.348* | 0.114 | 0.096 |
| 97 | 100 | 0.257 | 0.427* | 0.486* | 0.237 | 0.406* | 0.071 | 0.213 |
| 98 | 75 | 0.296 | 0.422* | 0.573* | 0.164 | 0.547* | 0.040 | 0.223 |
| 99 | 100 | 0.257 | 0.360* | 0.340* | 0.119 | 0.489* | 0.074 | 0.033 |
| 100 | 100 | 0.257 | 0.287* | 0.265* | 0.069 | 0.366* | 0.038 | 0.085 |
| 101 | 100 | 0.257 | 0.534* | 0.382* | 0.207 | 0.688* | 0.278* | 0.146 |

TABLE 4

SUMMARY OF THE NUMBERS OF CORRELATION COEFFICIENTS FOUND TO BE STATISTICALLY SIGNIFICANT AT THE 0.99 LEVEL OF CONFIDENCE

| | | | | | |
|---|---|---|---|---|---|
| Zero-order correlation coefficients with $N$-2 d.f. | | | | | |
| $r_{12}$ | $r_{13}$ | $r_{14}$ | $r_{23}$ | $r_{24}$ | $r_{34}$ |
| 61 | 65 | 18 | 72 | 2 | 7 |
| First-order partial correlation coefficients with $N$-3 d.f. | | | | | |
| $r_{12.4}$ | $r_{13.4}$ | $r_{14.2}$ | $r_{23.4}$ | $r_{24.3}$ | $r_{34.2}$ |
| 58 | 64 | 15 | 71 | 1 | 3 |
| Second-order partial correlation coefficients with $N$-4 d.f. | | | | | |
| $r_{12.34}$ | $r_{13.24}$ | $r_{14.23}$ | $r_{23.14}$ | $r_{24.13}$ | $r_{34.12}$ |
| 34 | 36 | 12 | 60 | 0 | 2 |

each other is not greatly affected by the number of vertebrae. Sixty of the coefficients, $r_{23\cdot14}$, are significant and this amounts to about 83 percent of the zero-order coefficients $r_{23}$, which were seen to be significant. The relationship between vertebrae and spines persists to a considerable extent regardless of the number of soft rays in the dorsal and anal fins. In the coefficients $r_{12\cdot34}$ and $r_{13\cdot24}$, we see that the relationships between vertebrae and rays of either the dorsal or anal fin are considerably diminished with respect to their zero-order counterparts. This is reasonable since the intimate relationship between the two soft fins would indicate that to hold the value of one constant, the other would be restricted.

## DISCUSSION

Gosline (1947) reported a significant positive correlation between standard length and vertebral number in a large sample of restricted origin of a percid darter. He discussed such a correlation found in natural populations of several other species and considered a number of factors that might be responsible. The most reasonable explanation would seem to be Tester's (1937). Tester found a similar correlation in the Pacific herring, and pointed out that where a positive correlation between length and vertebral count had been observed, it was found only within a given year class in a species that spawns in spring, during rising temperatures. Hence, larger (older) fish would have passed phenocritical periods at lower temperatures than the smaller animals.

Only four collections in the present work show a significant correlation between length and vertebral count, and of these, three were taken in April of the first year and one in February of the second year (Table 1, collections 9, 12, 14, and 40). If these fish are estimated to be 2 to 4 months advanced beyond vertebral phenocritical periods, then although the two characters are negatively correlated, they agree with Tester's conclusion very well; i.e., spawnings which gave rise to these collections would have taken place during a period of falling temperatures (Figure 3).

In a study of meristic characters of a stock of medaka, *Oryzias latipes*, Ali and Lindsey (1974) concluded that the extent of heritable variation observed at a given developmental temperature was approximately the same as the extent of ecophenotypic variation that could be induced by different developmental temperatures. However, in the interests of conservatism, the data in the present study are approached with the hypothesis that the observed variation has resulted from early developmental environment. Although a number of physical conditions attending early development are known to affect meristic character expression, in the setting of the present study, temperature seems to be the environmental factor most likely to have resulted in the conditions observed. In the following discussion, effects deduced to have been caused by developmental environment are ascribed to thermal history.

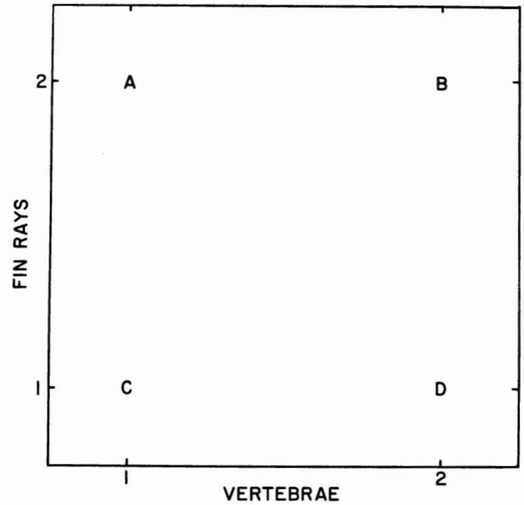


FIGURE 6. Array of hypothetical environmental conditions that would result in different correlative relationships between two meristic characters. *A*, warm through first (vertebral) phenocritical period, changing to cold through second (soft ray) phenocritical period; *B*, cold throughout both phenocritical periods; *C*, warm throughout both phenocritical periods; *D*, cold through first phenocritical period, changing to warm through second phenocritical period.

At the two stations sampled throughout the seasons of arrival of the young fish, the data (Table 2 and Figure 4) show numerous instances of year to year or month to month differences. Presumably, these reflect differences in thermal histories.

Figure 3 aids in visualizing the temperature gradient over at least some portion of the range of latitude considered. In Figure 1 a conspicuous cline in vertebral number is apparent only over the southern portion of the range. Data in Table 2 yield similar figures of clines in numbers of rays in the anal and soft dorsal fins. The cline might be a reflection of a temperature gradient, accentuated by greater isolation of local populations than among the four northern stations.

In Figure 6, consider that if the phenocritical periods of two characters occur at the same time, then stable temperatures give the greatest chance of obtaining collections including fish from conditions of only *C* and *B*. Such a collection would show a positive correlation between counts of the two characters. Under conditions approximating thermal stability and with temporal proximity of the phenocritical periods, only rarely would a collection include specimens from conditions *A* or *D*, and such inclusion would tend to cause a breakdown in the positive correlation. If a correlation (for example, $r_{12}$) were diminished due to inclusion of either *A* or *D* along with *B* and *C*, the variance of one or both of the characters would be considerably diminished. However, the data do not indicate this. Therefore, a loss of significance of $r_{12}$ must be due to inclusion of fish from both *A* and *D* conditions as well as from conditions *B* and *C*. This means conditions *A* and *D* must occur fairly frequently in nature, because, for example, the coefficient $r_{12}$ is not significant in 20 of the 81 collections (see Table 3). Hence, we should occasionally expect to find a negative coefficient that would result if a given collection were comprised of fish partially originating under condition *A* and partly under condition *D*. However, among the 486 coefficients in Table 3, 225 positive coefficients are significant, but none of the negative values is significant.

If conditions were stable and origins similar throughout the phenocritical periods so that a given sample contained fish originating under only one of conditions *A*, *B*, *C*, or *D* (Figure 6), then any variation observed could not be ascribed to the developmental environment. Hence, if natural conditions are stable, any observed variances of, and correlations between, characters would seem to indicate genetic relationships.

In some years of the seasonal study there is evidence of a month to month directional trend in condition of a given character. This might mean such trends have resulted in some of the positive correlations. If this is true, the variances might be expected to be unusually high in these collections. However, examination of the data discloses no systematic relationship between degree of positive correlation and degree of variation.

If the phenocritical periods of two characters coincide, any collection of fish including representatives of different constant thermal histories will show a positive correlation between conditions of these two characters. The most consistent relationship found ($r_{23}$) correlates number of rays in the anal fin with number of rays in the dorsal fin. It seems reasonable that this high degree of correlation indicates that the phenocritical periods of the two characters occur at about the same developmental time. These two periods do not coincide precisely, as indicated by the fact that in 9 of the collections, $r_{23}$ is not statistically significant and in 16 collections we find the number of vertebrae to be correlated with the number of rays of one fin but not the other. Over 75 percent of the coefficients, $r_{12}$ and $r_{13}$, are significant; this might be taken to indicate that the phenocritical periods of vertebrae and rays of the two fins occur at about the same time. However, examination of the summaries in Table 4 shows that the relationship between ray counts of the two soft fins is not greatly dependent on the number of vertebrae. Of the 72 significant correlations ($r_{23}$) between ray counts of the two soft fins, 60 of the coefficients, $r_{23 \cdot 14}$, are significant. Therefore, the phenocritical period of the vertebral column must be well removed in time from the phenocritical periods of the two soft fins. Hence, at least occasionally, significant negative values should be found among the coefficients $r_{12}$ and $r_{13}$, but they do not occur.

Note that the relationship between the two soft fins is independent of vertebral number. This indicates that the rays of these two fins do not set up simply on the basis of available segmental positions.

An examination of the relationships between number of spines in the dorsal fin and counts of the other three characters is informative. Table 3 shows 18 significant correlations between vertebral number and number of dorsal spines ($r_{14}$), but only 7 values of $r_{34}$ and 2 values of $r_{24}$. Since the number of spines shows a considerable degree of relationship to the number of vertebrae but little to the number of rays in the soft fins, we might conclude that a phenocritical period of spines occurs considerably earlier than the phenocritical period of the vertebral column.

This would place such a period much earlier than gastrulation, a conclusion that is not satisfactory. Results from the latitudinal study indicate that the number of spines is little affected by developmental temperature (see Figure 2). We cannot conclude that a phenocritical period of spines coincides with, or comes later than, that of vertebrae. This would result in appearance of a greater degree of relationship between spines and rays in the soft fins because the soft rays seem to be affected by temperature to about the same degree as the vertebrae. Since spines appear to be related to the soft fins to such a slight degree, the relationship between vertebrae and spines must be due to something other than developmental environment. It would seem most reasonable that these two characters, vertebrae and spines, are in some way genetically affiliated.

Each collection came from a single locality and in spite of the environmental vicissitudes implied by the data, there are no significant negative correlations between any two of the four characters. Hence, it seems probable that the positive relationships shown by the correlations are, in the aggregate, an expression of genetic affinities of the characters and to a lesser extent an expression of developmental environment. In fact, it appears probable that the positive correlative relationships are more likely to have been broken down by developmental environment than to have been enhanced by it. This is strongly implied by the findings concerning length, where only 4 of the 81 collections were found to show a significant correlation between this variable and vertebral count. First-order partial correlation coefficients, $r_{12\cdot5}$, were calculated for each of these 4 collections. Three of them (9, 12, and 14) gave coefficients of 0.279, 0.361, and 0.341, respectively. With $N$-3 d.f., these are highly significant. Hence, the correlation between vertebral count and number of anal rays is not dependent on length. If we take length as a correlate of thermal history, the relationship between vertebrae and anal rays must be independent of thermal history.

Collection 40 yielded a first-order correlation coefficient, $r_{12\cdot5}$, of 0.266; with $N$-3 d.f. this is not statistically significant. Hence, of the 81 collections only this one could be taken as evidence for a position contrary to the conclusions of this study.

The median meristic characters under discussion must all be intimately related to segmentation. The most reasonable conclusions drawn from the data seem to be as follows: The general strong positive correlations that exist between the characters indicate that in some way they are all genetically related. Temperature surrounding the very early development can be expected to approximate the selected spawning temperature, and as Strawn (1961) suggested, this selection must have at least some degree of genetic basis. The number of dorsal spines appears to be unaffected by environmental conditions attending natural development. The number of vertebrae appears to be susceptible to environmental conditions, presumably conditions surrounding early development. Hence, although the data show substantial departure from correlation between vertebral and dorsal spine counts, a definite positive relationship exists in spite of environmentally imposed distortions of vertebral counts. It seems safe to assume that the phenocritical period of the soft dorsal fin occurs considerably later than gastrulation, and the phenocritical period of the anal fin, later still. Therefore, with the lapse of time, the correlations between counts of these fins and numbers of vertebrae will be diminished by accumulating environmental vagaries. The correlation that might be expected between numbers of soft fin rays and dorsal spines virtually disappears due to the same causes, extending over an even longer period of time.

If these correlations are accepted as representing (within limits) genetic affinities, then the variation in the natural population must also be a genetic expression. As noted previously, the variances are strikingly similar, with the exception of the southernmost station. It is interesting and seems significant that Hubbs (1921) regarded this locality as approximating the juncture of the ranges of two distinct subspecies. The evidence is abundant in support of the conclusion of Heuts (1949) and Strawn (1961) that a high degree of variation in meristic counts among laboratory-reared fish is ecophenotypic, reflecting an unfavorable developmental environment. However, the variation among fish in a natural population will be a residuum from the effects of natural selection. In contrast with the variance among laboratory-reared animals, consistency of the variance in the many samples of wild fish in the present study indicates that this condition is intimately related to survival.

Based on studies of a number of species, Hubbs (1922:371) concluded, "clearly the same sort of variations as are induced by altered environmental conditions do characterize genetically distinct local races of fishes." Hubbs (1926:76) also recognized that the apparently minor morphological differences under discussion are related to functional differences, which are related to survival value, when he stated, "many of these structural consequences of physiological adaptations are among those characters of high systematic value long thought to be specifically devoid of adaptational significance."

The widespread, consistent inter- and intraspecific relationships between meristic character counts and temperature in nature indicate that both are visible indicators of mechanisms intimately related to survival value. Differences between taxa represent an accumulation of the effects of selection which necessarily are confined to mutant forms that make a viable developmental adjustment to a given set of environmental circumstances.

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## LITERATURE CITED

ALI, M. Y., and C. C. LINDSEY. 1974. Heritable and temperature-induced meristic variation in the medaka, *Oryzias latipes*. Can. J. Zool. 52(8):959–976.

CLOTHIER, C. R. 1950. A key to some southern California fishes based on vertebral characters. Calif. Dept. Nat. Res. Fish Bull. 79, 83 pp.

GOSLINE, W. A. 1947. Some meristic characters in a population of the fish *Poecilichthys exilis*: Their variation and correlation. Occ. Pap. Mus. Zool., Univ. Mich. No. 500, 23 pp.

HEINCKE, F. 1898. Naturgeschichte des Herings. I. Die Lokalformen und die Wanderungen des Herings in den europäischen Meeren. Abh. deut. Seefisch. Ver. 2(1): 1–128.

HEUTS, M. J. 1949. Racial divergence in fin ray variation patterns in *Gasterosteus aculeatus*. J. Genetics 49:183–191.

HUBBS, C. L. 1921. The latitudinal variation in the number of vertical fin-rays in *Leptocottus armatus*. Occ. Pap. Mus. Zool., Univ. Mich. No. 94, 7 pp.

———. 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. Am. Naturalist 56:360–372.

———. 1926. The structural consequences of modifications of the developmental rate in fishes correlated with the temperature of water during development. Am. Naturalist 60:57–81.

———, and C. HUBBS. 1953. An improved graphical analysis and comparison of series of samples. Syst. Zool. 2(2):49–57.

JONES, A. C. 1962. The biology of the euryhaline fish *Leptocottus armatus armatus* Girard (Cottidae). Univ. Calif. Pub. Zool. 67(4):321–368.

JORDAN, D. S. 1891. Relations of temperature to vertebrae among fishes. Proc. U.S. Nat. Mus. 14: 107–120.

KUJALA, N., and B. WYATT. 1961. Surface temperature and salinity observations at shore stations on the Oregon coast. Data Rep. No. 12, Dept. Oceanogr., Ore. State Univ. 23 pp.

LINDQUIST, A. 1968. Meristic and morphometric characters, year-classes and races of the sprat (*Sprattus sprattus*). Inst. Mar. Res. Lysekil Ser. Biol. Rep. 17: 1–26.

LINDSEY, C. C. 1954. Temperature controlled meristic variation in the paradise fish *Macropodus opercularis* (L.). Can. J. Zool. 30: 87–98.

MAYR, E. 1963. Principles of Systematic Zoology. McGraw-Hill, New York.

OLIPHANT, M., B. WYATT, and N. F. KUJALA. 1962. Surface temperature and salinity observations at shore stations on the Oregon coast for 1961. Data Rep. No. 8, Dept. Oceanogr., Ore. State Univ. 16 pp.

ORSKA, J. 1962. The influence of temperature on the development of meristic characters of the skeleton in Salmonidae. Part I. Temperature-controlled variations of the number of vertebrae in *Salmo irideus* Gibb. Zool. Polon. 12(3): 309–339.

PEARCY, W. G., and S. S. MYERS. 1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish. Bull. U.S. 72(1): 201–213.

SCHMIDT, J. 1917. Racial investigations. II. C. R. Lab. Carlsberg 14(1): 11–17.

———. 1919. Racial investigations. III. C. R. Lab. Carlsberg 14(5): 1–7.

———. 1920. Racial investigations. V. C. R. Lab. Carlsberg 14(9): 1–14.

———. 1921. Racial investigations. VII. C. R. Lab. Carlsberg 14(15): 19–23.

SCRIPPS INSTITUTION OF OCEANOGRAPHY. 1960. Surface water temperatures at shore stations United States west coast and Baja California 1956–1959. SIO Ref. 60-27.

———. 1961. Surface water temperatures at shore stations United States west coast and Baja California. SIO Ref. 61-14.

———. 1962. Surface water temperatures at shore stations United States west coast and Baja California. SIO Ref. 62-11.

———. 1963. Surface water temperatures at shore stations United States west coast and Baja California. SIO Ref. 63-17.

SNEDECOR, G. W. 1946. Statistical methods. Iowa State College Press, Ames.

STILL, R., B. WYATT, and N. KUJALA. 1963. Surface temperature and salinity observations at shore stations on the Oregon coast for 1962. Data Rep. No. 11, Dept. Oceanogr., Ore. State Univ. 15 pp.

STRASSBURG, D. W. 1955. North–south differentiation of blenniid fishes in the central Pacific. Pac. Sci. 9(3): 297–303.

STRAWN, K. 1961. A comparison of meristic means and variances of wild and laboratory-raised samples of the fishes, *Etheostoma grahami* and *E. lepidum* (Percidae). Texas J. Sci. 13(2): 127–159.

TÅNING, A. V. 1952. Experimental study of meristic characters in fishes. Biol. Rev. 27: 169–193.

TESTER, A. L. 1937. Populations of herring (*Clupea pallasii*) in the coastal waters of British Columbia. J. Biol. Bd. Can. 3: 108–144.